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Body condition and clutch desertion in penduline tit *Remiz pendulinus*

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Summary

Parental care is costly since it takes time and energy, and whilst caring the parent may be predated. The benefits of care (i.e., viable offspring) however, are shared equally between the genetic parents: the male and the female. Thus a conflict occurs between the parents over care in many multiple-brooding animals, since each parent prefers the other to do the hard work of raising young ('sexual conflict over care'). One of the most striking examples of this conflict occurs in a small passerine bird, the penduline tit *Remiz pendulinus* in which both the male and the female may sequentially mate with several mates within a single breeding season. Incubation and brood-rearing are carried out by a single parent (either the male or the female). However, about 30% of clutches are abandoned by both parents. We investigated how body condition may influence parental behaviour of male and female penduline tits. We show that three measures of body condition (body mass, fat reserves and haematocrit value) are consistent with each other for males, although not for females. Nest building appears to be energetically more demanding than incubation in both sexes. In line with this, we found that males and females in good condition deserted their clutch more often than males and females in poor condition. Individuals in poor condition may care because incubation is energetically less expensive than nest building, and they cannot afford the energy requirement of building a new nest. We argue that understanding body condition in the context of parental care is both challenging and essential, since mathematical models (single-parent optimisation models and game-theory models) provide conflicting predictions. Future work, preferably by experimentally manipulating the body condition of penduline tits, is needed to test how body condition influences caring/deserting decisions in this puzzling avian system.

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Introduction

In most socially monogamous birds the male and female contribute to parental activities, such as nest building, incubation or nestling feeding. However, the relative contribution by the sexes to these activities varies both across and within species (Clutton-Brock, 1991; Balshine-Earn et al., 2002), and these differences remain poorly understood (Ketterson & Nolan, 1994).

The amount of care provided by one parent depends on several factors. First, the level of parental effort to a reproductive activity is expected to be state-dependent because reproductive decisions have energetic consequences (Webb et al., 2002). Second, the level of care by one parent depends on the amount of care by its social mate, with a reduction in effort by one parent often resulting in partial compensation by the other parent (Wright & Cuthill, 1989, 1990; McNamara et al., 1999; Limbourg et al., 2004). Assuming that individuals try to minimize energetic expenses, both parents' interest is to reduce its own contribution and lower its own costs, but this is constrained by the capability of its mate to compensate this loss. Theoretical models predict that a parent is more likely to provide care if its mate has a lower body condition (Barta et al., 2002). For example, in many bird species incubation is costly in terms of elevated energetic cost of heat production to maintaining adequate egg temperatures (e.g., Williams, 1996; Bryan & Bryant, 1999; Tinbergen & Williams, 2002), and in terms of time that could otherwise be used for foraging and mate searching/mating (Bryan & Bryant, 1999; Eikenaar et al., 2003). Therefore, incubation may reduce body condition and thus may be in trade-off with subsequent survival and future reproduction (Reid et al., 2000; Visser & Lessells, 2001). Consequently, individuals of better body condition are expected to allocate more resources into caring than individuals of poor body condition, since they have higher reserves to spare. Third, the amount of parental care might also depend on future reproductive prospects, such as pursuing additional matings (Westneat et al., 1990; Magrath & Komdeur, 2003; Houston et al., 2005). Thus to understand why individuals care whereas others do not, we need to know the relative benefits of both caring and deserting (Székely et al., 1996, 1999). These benefits are likely to depend on the state of the animal, such as its body condition, age or experience (Houston & McNamara, 1999).

The influence of body condition on parental decisions is expected to occur in small animals that have limited energy reserves and variable parental care. We studied one such species, the penduline tit (*Remiz pendulinus*). This small migratory passerine bird (body mass about 10 g) breeds in marshes, gallery forests and fish-ponds between Western Europe and China (Cramp et al., 1993). Among birds, penduline tits have an exceptionally diverse mating system in which both sequential polygyny and sequential polyandry occur in the same population (Franz & Theiss, 1983; Persson & Öhrström, 1989; Franz, 1991). Males build elaborate hanging nests to attract females (Hoi et al., 1994; Szentirmai et al., in press). After pair formation and egg laying, but before the onset of incubation, either one parent or both parents desert the clutch. The remaining parent take over the full responsibility for the clutch, or if both parents desert, the current reproductive success of both will be zero (Hoi et al., 1994). Parental care is variable since incubation and chick rearing can be provided either only by the female (50-70% of clutches) or the male (5-20% of clutches), whereas both parents desert 30-40% of clutches (Franz & Theiss, 1983; Persson & Öhrström, 1989; Franz, 1991). On the one hand, if the male deserts the nest, he often builds a new nest to attract a new mate whilst his previous female incubates the eggs and raises the young. On the other hand, if the female deserts the clutch, she may remate after desertion and thus lay more eggs with different mates. This 'battle of the sexes' (Franz & Theiss, 1983; Houston et al., 2005) appears to be an obvious example of sexual conflict over care.

Our study was designed to answer two questions. First, do nest building and incubation influence body condition of male and female penduline tits? We use three measures of body condition; haematocrit value, amount of subcutaneous fat and body mass. Second, does body condition of the male influence his and his mates' parental decisions? To answer this question we compare male body condition during nest building with his and his social mate's decision to care for the clutch. In line with a recent optimisation model (Webb et al., 2002) we predicted that males in good condition should care for the clutch whereas males in bad condition should desert.

Methods

Study site and population monitoring

We investigated the penduline tits at Fehértó, South Hungary (46°19'N, 20°5'E) in 2002 (5 April - 2 August), 2003 (15 April - 22 August), and 2004 (21 April - 2 August). Fehértó is an extensive fishpond system (1,321 ha), where approximately 90 males and 50 females bred each year on the dykes separating the fishpond units. The study area was searched for nests every second day and we found all nests ($N = 229$) during nest building.

Males and females were caught either by mist net and song playbacks, or by catching the incubating parent in their nest with a nest trap. In total 145 males and 18 females were caught during nest building, and 7 males and 59 females during incubation. Each individual was ringed using a unique combination of three colour rings and a metal ring of the Hungarian Ornithological Institute. During capture, birds that were not already ringed were individually colour banded, and weighed to the nearest 0.1 g using a 30 g Pesola spring balance. Birds were sexed using plumage characters. Tarsus and wing lengths were measured to the nearest 0.1 mm using vernier callipers and to the nearest 1 mm using a ruler, respectively. Tarsus and wing length were measured three times, and the mean value was used in the analyses. The bird's subcutaneous fat reserves (hereafter fat score) were also scored at a scale from 0, no fat, to 8, high fat (for methodology, see Bairlein, 1995). In addition, of each bird caught in 2003 (45 males and 18 females) haematocrit was measured. Haematocrit was assessed by taking a 50-100 μ l blood sample from the bird's brachial vein and storing it in a heparinized blood capillary. The non-heparin-end of the capillary was closed with clay and the samples were kept in a styrene-foam cooling box during transport from the field site to the laboratory to avoid clotting. The samples were centrifuged for 10 minutes at 9,000 rotations per minute within an hour after catching. The two columns in the capillary, packed red blood cells and total blood plasma, were measured three times each to the nearest 0.1 mm using vernier callipers. The mean length of each column was used in the analyses. The haematocrit value is calculated as packed red blood cell volume divided by total blood plasma volume. We were not able to calculate the repeatabilities of haematocrit measurements, since only one blood sample per individual was taken due to their small body size. However, haematocrit measurements

in other species were highly repeatable (90-99%; e.g., Ots et al., 1998; Potti et al., 1999).

Males were visited for 15 minutes every second day to establish the date of mating, the onset of incubation, and parental care decision of male and female (care/desert). A male was considered mated when he built his nest together with a female, and/or copulated with a female at his nest (following Szentirmai et al., in press). Mated pairs were visited for 15 minutes every second day until one parent (or both of them) deserted the clutch. Since desertion occurs before incubation commences and at that time the staying parent is still building the nest, 15 minutes were sufficient to establish the absence (desertion) of either or both partners (I. Szentirmai, pers. obs.). Desertion was recognised if the parent was not seen at the nest for at least two days (Szentirmai et al., in press).

Statistical analyses

Observations involved a single nest for each male and female to avoid pseudoreplications. Body mass of males significantly increased with tarsus length, and body mass of females tended to increased with tarsus length (Pearson correlations: males: $r_p = 0.158$, $N = 158$, $p = 0.023$; females: $r_p = 0.174$, $N = 90$, $p = 0.110$); therefore we included tarsus length as a covariate in the analyses of body mass (Green, 2001). Body mass and haematocrit were normally distributed, whereas fat score was skewed, therefore we either used non-parametric statistics, or parametric statistics with the ranks of the fat score. The latter approach is appropriate in a factorial design as long as both factors have two levels (i.e., 2×2 , see Seaman et al., 1994). In the analyses of the relationships between different measures of body condition, we pooled data from both nest-building and incubating penduline tits. We used General Linear Models (GLMs) to analyse the change in body mass (dependent variable) between nesting stages (factor 1: nest building or incubation) and sex (factor 2: male or female). Tarsus length was also included as a covariate in these GLMs. Since the assumption for the homogeneity of variances was not fulfilled for haematocrit, and fat score was not normally distributed we analysed the ranks of these two variables (dependent variable) in two-way ANOVAs (factor 1: nest building or incubation; factor 2: male or female) (Seaman et al., 1994). We used binary logistic regressions to analyse the effect of the body condition of males and females during nest building on their parental care decision (care/desert).

We used SPSS v. 11.0 (SPSS, 2001) for statistical analyses. Means are expressed with standard errors, probability values are two-tailed and the null hypothesis was rejected at $p < 0.05$.

Results

Relationships between measures of body condition

Body mass of males increased with fat score (partial rank correlations controlling for tarsus length: $r = 0.29$, $df = 147$, $p < 0.001$; Figure 1a). Their haematocrit value decreased with body mass (partial rank correlation controlling for tarsus length: $r = -0.49$, $df = 41$, $p = 0.001$; Figure 1b), whereas it was not significantly related to fat score (Spearman rank correlation: $r_s = -0.19$, $N = 43$, $p = 0.218$; Figure 1c). Body mass of females also increased with fat score ($r = 0.26$, $df = 83$, $p = 0.017$, Figure 1a), whereas their haematocrit value was neither related to body mass nor to fat score (body mass versus haematocrit value controlling for tarsus length: $r = -0.25$, $df = 17$, $p = 0.310$, Figure 1b; fat score versus haematocrit value: $r_s = -0.06$, $N = 20$, $p = 0.801$, Figure 1c).

Body condition during nest building and incubation

Body mass of females was significantly higher than body mass of males (GLMs: $F_{1,210} = 20.54$, $p < 0.001$; Figure 2a). Both males and females were heavier during incubation than during nest building ($F_{1,210} = 10.66$, $p = 0.001$; Figure 2a). Similarly, females had higher fat scores than males (two-way ANOVA: $F_{1,213} = 56.85$, $p < 0.001$; Figure 2b), and both males and females had significantly higher fat scores during incubation than during nest building ($F_{1,210} = 19.30$, $p < 0.001$; Figure 2b).

A significant interaction between sex and nesting stage (two-way ANOVA, $F_{1,57} = 6.39$, $p = 0.014$; Figure 2c) indicated that haematocrit values of sexes changed differently between nesting stages. In males, haematocrits declined whereas in females no change is apparent. Neither the effect of sex ($F_{1,57} = 2.94$, $p = 0.092$; Figure 2c) nor of nesting stage was significant ($F_{1,57} = 0.74$, $p = 0.393$).

Body mass of nest building males decreased and their fat scores tended to decrease with the number of days from the start of nest building (Spearman

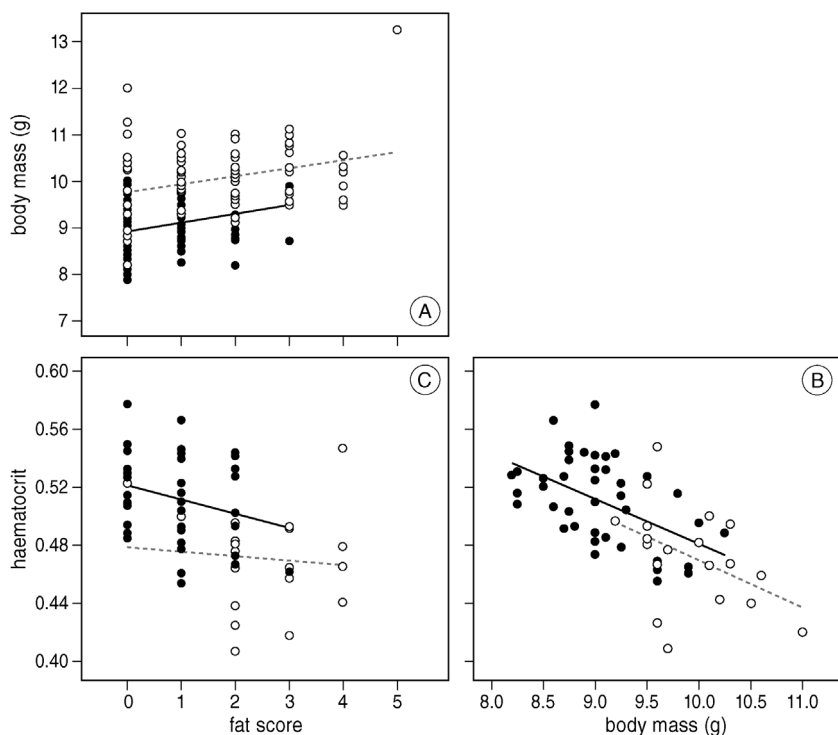


Figure 1. Relationships between different measures of body condition of male (filled symbols and solid lines) and female (open symbols and dashed lines) penduline tits. (a) Fat scores and body mass, (b) body mass and haematocrit, (c) fat score and haematocrit.

rank correlations: body mass: $r_s = -0.18$, $N = 135$, $p = 0.034$; fat score: $r_s = -0.16$, $N = 136$, $p = 0.065$). Haematocrit of nest building females was not related to the number of days from the start of nest building ($r_s = -0.019$, $N = 38$, $p = 0.911$).

Neither body mass, nor fat score, nor haematocrit of incubating males and females changed significantly with the number of days from the start of incubation (Spearman rank correlations: $p > 0.20$ for all correlations).

Influence of male body condition on parental decisions

Of the males measured during nest building and which attracted a mate, 10 cared and 70 deserted the clutch. Males with higher body mass deserted their clutches more often than males with lower body mass (logistic regression: body mass: $\chi^2_1 = 4.106$, $p = 0.043$; tarsus length: $\chi^2_1 = 1.465$, $p =$

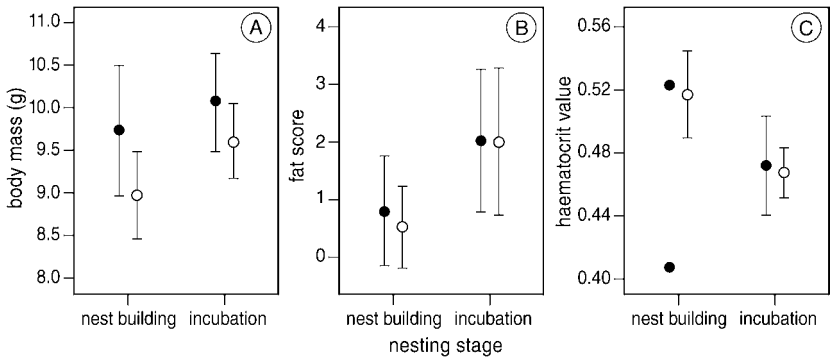


Figure 2. Mean (\pm SE) body condition of male (○) and female (●) penduline tits during nest building and incubation: (a) body mass (2002–2004), (b) fat score (2002–2004), (c) haematocrit value (for the two nest building females the exact values are shown; 2003).

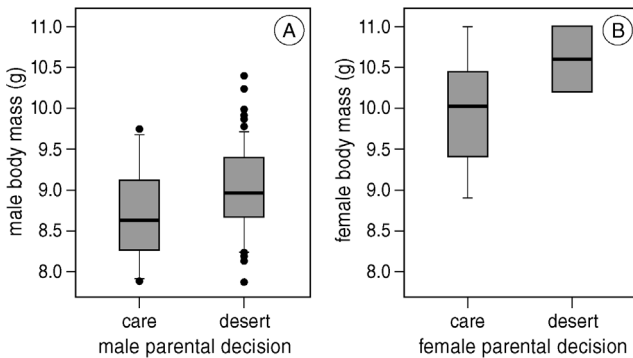


Figure 3. Body mass of nest building male (a) and female (b) penduline tits in relation to their subsequent parental decision (see also Table 1). The lines in the boxes are drawn across the median and the bottom and the top of the boxes are the lower and upper quartiles, respectively. Lower and upper whiskers represent 10th and 90th percentiles, respectively.

0.226; Figure 3a), whereas their fat score was not related to parental decision ($\chi^2_1 = 0.010$, $p = 0.919$). Since we measured the body mass and fat score of only one female during nest building who's mate did not desert, we did not analyse whether female condition influenced the male's subsequent parental decision. Similarly, we had only few data on the relationship between male or female haematocrit and male parental decision.

Of the females measured during nest building 9 cared and 3 deserted the clutch. Females deserted their clutch more often if their body mass was higher (Figure 3b, Table 1), and tended to desert more often if their fat scores

Table 1. The influence of body condition (body mass, fat score and haematocrit value) of male and female penduline tits on the parental care decision of females. The results of two logistic regression models are shown, in which the decision by the female was the dependent variable (3 caring and 9 deserting females), and body mass, tarsus length, fat score and haematocrit value of males or females were covariates.

Covariates	Female parental care decision			
	Male condition		Female condition	
	χ^2_1	<i>p</i>	χ^2_1	<i>p</i>
Body mass	0.280	0.596	8.095	0.004
Tarsus length	1.371	0.242	2.626	0.105
Fat score	2.314	0.128	2.879	0.090
Haematocrit	1.371	0.242	–	–

were higher (Table 1). We had no data to analyse the relationship between haematocrit of nest building females and their subsequent parental decision. Parental decision of females was not related to the body condition of their mates during nest building (Table 1).

Discussion

Our study of state-dependent parental care decisions in penduline tits provided three key results. First, we found a positive correlation between body mass and fat score, and a negative correlation between haematocrit and body mass. These results are consistent with previous studies in that the haematocrit signals intense work load and thus high oxygen and energy consumption (Saino et al., 1997; Horak et al., 1998; Piersma et al., 2000). Other studies, however, failed to find this relationship (Sealander, 1962; Villegas et al., 2002). If the haematocrit signals the state of workload, variation in this measure between studies may be due to differences in the extent of workloads during which the condition measures were taken, but also due to differences in storage and usage of food and fat reserves during life history (Kooijman, 2000).

Second, reproductive stage was significantly associated with body condition (body mass and fat score) of both males and females, although the effect was larger in males than in females. Interestingly, both males and females

were in better condition during incubation than nest building. A potential explanation for this difference is that collecting, transporting and using nest materials are energetically more expensive than incubation. On the one hand, male penduline tits do most of the building and spend up to 40% of their time building their complex nests (Szentirmai et al., in press). Females also contribute to nest building, although they mostly stay inside the nest and weave the nest materials into the nest by stitching movements. Some nest materials are brought from distant locations; for instance we observed males to fly out their territory in search of suitable nest materials. On the other hand, incubation appears not to be expensive in penduline tits. There is an ongoing debate whether incubation is costly in birds (Piersma & Morrison, 1994; Bryan & Bryant, 1999; Thomson et al., 1998; Reid et al., 2002), thus an experimental test of this idea is highly desirable. Nevertheless, given that the nest is well-insulated (Hoi et al., 1994; Grubbauer & Hoi, 1996; I. Szentirmai, T. Székely & A. Liker, unpubl. data) and egg temperatures only drop slowly after the parent left the nest (P. Horváth, unpubl. data), we conjecture that the incubation is not very costly in penduline tits. Note however, that we had no data from brood-rearing which may well be an energetically expensive behaviour.

Finally, we found that males in good condition deserted their clutch more often than males in poor condition. Males in poor condition may care because incubation is energetically less expensive than nest building, and because they can't afford the energy requirement necessary for building another nest. In agreement with our findings for males, we found that females in good condition deserted their clutch more often than females in poor condition. The above results are consistent with the interpretation of desertion as an outcome of sexual conflict. In penduline tits both sexes can increase their reproductive success by abandoning the clutch and mate (Persson & Öhrström, 1989; Székely et al., 1996). The deserting parent gains two major benefits: (i) remating and reproducing with a new mate, and (ii) he/she dispenses with the energetic costs of incubation and brood-rearing. Previously we showed that males with larger ornament (as indicated by the size of their eye-stripe) had significantly higher body condition and found a new mate sooner than less ornamented ones, thus our current result suggests that males in better body condition are better able to attract a new female than males in poor body condition. Testing the latter prediction would be particularly interesting, since the relationship between body condition and parental care is

more complex than usually assumed (Webb et al., 2002). Given that the male deserts, the female may be constrained. If she cares for the brood, she will spend up to 4 weeks incubating the clutch and feeding the chicks herself. If, however, she abandons the clutch, she dooms the full reproductive effort to failure. Whilst these scenarios present a sequential decision (male first and then female), in reality the parents may monitor each other's behaviour and they may be able to predict the future moves of their mate. The latter issue is important for both theoretical and empirical understanding of parental care patterns (R.E. van Dijk, I. Szentirmai, T. Székely, J. Komdeur, unpubl. data; Houston et al., 2005).

Concluding remarks

Our work on the penduline tit shows that three measures of body condition are consistent with each other in males, although less strongly in females. Nest building appears to be energetically more demanding than incubation. In line with these results, males may be able adjust their parental care decision based on their current body condition. Future work, preferably by manipulating the body condition of male and female penduline tits, is needed to test how body condition relates to caring/deserting decisions. The latter issue is particularly interesting, since theoretical models provide different predictions with regards to body condition and parental care. For instance, Barta et al. (2002) predicted that female birds may strategically handicap themselves by reducing their own body condition. This would 'force' the male to stay with her. The female, however, may exploit the males' willingness to care and she deserts.

A major gap, however, in our current knowledge is the influence of behavioural strategies on reproductive success. For instance, do males in good condition produce more chicks than males in poor condition? Since male reproductive success depends on female behaviour (which in turn, being influenced by her own condition), the answer to this question is far from being trivial. Note also, that females play their own game (which may depend on their own condition and on the condition of their mate). To understand the outcome of these interactions we need comprehensive measures of reproductive success and a specific game-theoretic model for the penduline tit.

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References

- Bairlein, F. (1995). European-African songbird migration network: manual of field methods. — Wilhelmshaven, Germany.
- Balshine-Earn, S., Kempenaers, B. & Székely, T. (2002). Conflict and co-operation in parental care. Thematic issue. — *Phil. Trans. R. Soc. Lond. B* 357: 237-404.
- Barta, Z., Houston, A.I., McNamara, J.M. & Székely, T. (2002). Sexual conflict about parental care: the role of reserves. — *Am. Nat.* 159: 687-705.
- Bryan, S.M. & Bryant, D.M. (1999). Heating nest-boxes reveals an energetic constraint on incubation behaviour in great tits, *Parus major*. — *Proc. R. Soc. Lond. B* 266: 157-162.
- Clutton-Brock, T. (1991). The evolution of parental care. — Princeton University Press, Princeton, New Jersey.
- Cramp, S., Perrins, C.M. & Brooks, D.J. (eds) (1993). Handbook of the birds of Europe, the Middle East and North Africa. Birds of the western Palearctic. Vol. 7. — Oxford University Press, Oxford.
- Eikenaar, C., Berg, M.L. & Komdeur, J. (2003). Experimental evidence for the influence of food availability on incubation attendance and hatching asynchrony in the Australian reed warbler *Acrocephalus australis*. — *J. Avian Biol.* 34: 419-427.
- Franz, D. (1991). Paarungssystem und Fortpflanzungsstrategie der Beutelmeise *Remiz pendulinus*. — *J. Ornithol.* 132: 241-266.
- Franz, D. & Theiss, N. (1983). Brutbiologie und Bestandsentwicklung einer farbberingten Population der Beutelmeise *Remiz pendulinus*. — *Verh. Ornithol. Ges. Bayern* 23: 393-442.
- Green, A.J. (2001). Mass/length residuals: measures of body condition or generators of spurious results? — *Ecology* 82: 1473-1483.
- Grubbauer, P. & Hoi, H. (1996). Female penduline tits *Remiz pendulinus* choosing high quality nests benefit by decreased incubation effort and increasing hatching success. — *Ecoscience* 3: 274-279.
- Hoi, H., Schleicher, B. & Valera, F. (1994). Female mate choice and nest desertion in penduline tits (*Remiz pendulinus*): the importance of nest quality. — *Anim. Behav.* 48: 743-746.
- Horak, P., Ots, I. & Murumagi, A. (1998). Haematological health state indices of reproducing great tits: a response to brood size manipulation. — *Funct. Ecol.* 12: 750-756.

- Houston, A.I. & McNamara, J.M. (1999). Models of adaptive behaviour: an approach based on state. — Cambridge University Press, Cambridge.
- Houston, A.I., Székely, T. & McNamara, J.M. (2005). Conflict between parents over care. — Trends Ecol. Evol. 20: 33-38.
- Ketterson, E.D. & Nolan, V. Jr (1994). Male parental behavior in birds. — Ann. Rev. Ecol. Syst. 25: 601-628.
- Kooijman, S.A.L.M. (2000). Dynamic energy and mass budgets in biological systems, 2nd edn. — Cambridge University Press, Cambridge.
- Limbou, T., Mateman, A.C., Andersson, S. & Lessells, C.M. (2004). Female blue tits adjust parental effort to manipulated male UV attractiveness. — Proc. R. Soc. Lond. B 271: 1903-1908.
- Magrath, M.J.L. & Komdeur, J. (2003). Is male care compromised by additional mating opportunity? — Trends Ecol. Evol. 18: 424-430.
- McNamara, J.M., Gasson, C.E. & Houston, A.I. (1999). Incorporating rules for responding into evolutionary games. — Nature 401: 368-371.
- Ots, I., Murumagi, A. & Horak, P. (1998). Haematological health state indices of reproducing great tits: methodology and sources of natural variation. — Funct. Ecol. 12: 700-707.
- Persson, O. & Öhrström, P. (1989). A new avian mating system: ambisexual polygamy in the penduline tit *Remiz pendulinus*. — Ornis Scand. 20: 105-111.
- Piersma, T. & Morrison, R.I.G. (1994). Energy expenditure and water turnover of incubating ruddy turnstones: high costs under high arctic climatic conditions. — Auk 111: 366-376.
- Piersma, T., Koolhaas, A., Dekinga, A. & Gwinner, E. (2000). Red blood cell and white blood cell counts in sandpipers (*Philomachus pugnax*, *Calidris canutus*): effects of captivity, season, nutritional status and frequent bleedings. — Can. J. Zool. 78: 1349-1355.
- Potti, J., Moreno, J., Merino, S., Frias, O. & Rodriguez, R. (1999). Environmental and genetic variation in the haematocrit of fledgling pied flycatchers *Ficedula hypoleuca*. — Oecologia 120: 1-8.
- Reid, J.M., Monaghan, P. & Ruxton, G.D. (2000). Resource allocation between reproductive phases: the importance of thermal conditions in determining the cost of incubation. — Proc. R. Soc. Lond. B 267: 37-41.
- Reid, J.M., Monaghan, P. & Ruxton, G.D. (2002). Males matter: the occurrence and consequences of male incubation in starlings (*Sturnus vulgaris*). — Behav. Ecol. Sociobiol. 51: 255-261.
- Saino, S., Cuervo, J.J. & Krivacek, M. (1997). Experimental manipulation of tail ornament size affects the haematocrit of male barn swallows (*Hirundo rustica*). — Oecologia 110: 186-190.
- Sealand, J.A. (1962). Seasonal changes in blood values of deer mice and other small mammals. — Ecology 43: 107-119.
- Seaman, J.W., Walls, S.C., Wise, S.E. & Jaeger, R.G. (1994). Caveat-emptor: rank transform methods and interaction. — Trends Ecol. Evol. 9: 261-263.
- SPSS Inc. (2001). SPSS ver. 11.0. — Chicago, IL, USA.
- Székely, T., Cuthill, I.C. & Kis, J. (1999). Brood desertion in Kentish plover: sex differences in remating opportunities. — Behav. Ecol. 10: 185-190.
- Székely, T., Webb, J.N., Houston, A.I. & McNamara, J.M. (1996). An evolutionary approach to offspring desertion in birds. — In: Current ornithology, Vol. 13 (Nolan, V. Jr & Ketterson, E.D., eds). Plenum Press, New York, p. 271-330.

- Szentirmai, I., Komdeur, J. & Székely, T. (in press). What makes a nest-building male successful? Male behaviour and female care in penduline tits. — *Behav. Ecol.*
- Tinbergen, J.M. & Williams, J.B. (2002). Energetics of incubation. — In: *Avian incubation: behaviour, environment and evolution* (Deeming, D.C., ed.). Oxford Ornithological Series, p. 299-313.
- Thomson, D.L., Monaghan, P. & Furness, R.W. (1998). The demands of incubation and avian clutch size. — *Biol. Rev.* 73: 293-304.
- Villegas, A., Sanchez, J.M., Costillo, E. & Corbacho, C. (2002). Blood chemistry and haematocrit of the black vulture (*Aegypius monachus*). — *Comp. Biochem. Physiol. A* 132: 489-497.
- Visser, M.E. & Lessells, C.M. (2001). The cost of egg production and incubation in great tits (*Parus major*). — *Proc. R. Soc. Lond. B* 268: 1271-1277.
- Webb, J.N., Székely, T., Houston, A.I. & McNamara, J.M. (2002). A theoretical analysis of the energetic costs and consequences of parental care decisions. — *Phil. Trans. R. Soc. Lond. B* 357: 331-340.
- Westneat, D.F., Sherman, P.W. & Morton, M.L. (1990). The ecology and evolution of extra-pair copulations in birds. — *Curr. Ornithol.* 7: 331-369.
- Williams, J.B. (1996). The energetics of avian incubation. — In: *Avian energetics and nutritional ecology* (Carey, C., ed.). Chapman & Hall, New York, p. 355-406.
- Wright, J. & Cuthill, I. (1989). Manipulation of sex differences in parental care. — *Behav. Ecol. Sociobiol.* 25: 171-181.
- Wright, J. & Cuthill, I. (1990). Biparental care: short-term manipulation of partner contribution and brood size in the starling, *Sturnus vulgaris*. — *Behav. Ecol.* 1: 116-124.
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